Structures and Functions of the Endophallic Copulatory Tube in the Family Staphylinidae (Insecta: Coleoptera)

13

Shun-Ichiro Naomi

Abstract

This paper deals with the structures and functions of the endophallic copulatory tube in Staphylinidae, which has been previously called "copulatory piece," "endophallus," "flagellum," etc. in descriptive studies. First, the general morphology of the copulatory tube and the pseudocopulatory tube is discussed, together with the characterizations and terminology. Second, the distribution of the copulatory tubes in Staphylinidae is described. Third, the structures of the seven basic and some other unique forms of the copulatory tubes in Staphylinidae are described in detail, paying special attention to those of Steninae. Fourth, the functions of the copulatory tubes in Staphylinidae are described or hypothesized, paying special attention to those of Steninae. Namely, the function of the copulatory tube is simply a "spermatophore (or sperm) depositor" in some cases (e.g., some *Stenus*), whereas it has double function: a "spermatophore (or sperm) depositor" and an "extension tube (or sperm) guiding rod in some other cases (e.g., some *Aleochara*).

13.1 Introduction

In Coleoptera, the aedeagus consists externally of the tegmen and the median lobe; and the tegmen comprises of the phallobase (basal piece) and the parameres (lateral lobes) (Sharp and Muir 1912; Lawrence and Britton 1994). Since the phallobase is almost or completely missing in most species of Staphylinidae, the aedeagus consists of the median lobe and paired parameres (Crowson 1981); and in the median lobe, there is internal endophallus. The external and internal structures of aedeagi are highly diverse morphologically, and they are considered to be very useful both for classifying the species and also for classifying the species groups of genera in Staphylinidae; and thus, taxonomists have paid special attention to them when attempting to do the revisional studies of a group in question.

In Staphylinidae, the endophallus comprises of a copulatory tube, sclerites, sclerotized bands, etc.; and the copulatory tube is located inside a membranous reversible internal sac, and the latter connects the rim of the apical foramen (i.e., the

S.-I. Naomi (✉)
Natural History Museum and Institute, Chiba, Japan
e-mail: naostenus@hb.tp1.jp

O. Betz et al. (eds.), *Biology of Rove Beetles (Staphylinidae)*,
https://doi.org/10.1007/978-3-319-70257-5_13

ostium) with the base of the copulatory tube. The simple form of the endophallus is made up of a simple reversible internal sac. However, the endophallus very often includes the following three components: (a) paired expulsion hooks that have a function of triggering the copulatory tube, (b) paired longitudinal bands that have a function of reinforcing the membrane of the internal sac, and (c) a copulatory tube. These relatively complex endophalli are found in such genera as *Stenus* (Naomi 2006a, b; Naomi et al. 2017) and *Sepedophilus* (Naomi and Maruyama 1997). In some genera, e.g., *Scopaeus* (Frisch 1997, 1998, 1999), *Fenderia* (Puthz 2003a), and *Aploderus* (Shimada 2002), the endophallus is highly complex, because in addition to all or two of those three components, it is also armed with a variety of sclerites, tufts, and other structures. Crowson (1981:70) suggested that in some groups of Coleoptera, the sclerotizations of the endophallus may play a role in shaping a spermatophore, but the function of the endophallic sclerites in Staphylinidae still remains unclear in most cases.

Out of the various structures of the endophallus in Staphylinidae, the copulatory tube can be regarded as the structure that plays an important role in copulation, because it serves as a tube for transmitting the sperm or spermatophore to the vagina or spermatheca. Thus, it is worthy of studying from the morphological point of view. After Sharp and Muir (1912) first studied in detail the basic structures of the aedeagus in Coleoptera (including the Staphylinidae), Blackwelder (1936) and Naomi (1990) each studied the aedeagus of Staphylinidae in a comparative perspective. However, the endophallic copulatory tubes in Staphylinidae have not been so far studied in detail probably due to the three reasons described below.

First, not all staphylinids possess the copulatory tube as a component of the aedeagus. Second, the morphological diversity of the copulatory tubes is very high. For example, in some cases (e.g., some *Dianous*), it is composed of a very thick stick or rod; and thus, it looks as a different structure. In other cases, it is composed of a very long flexible, whiplike tube called "flagellum." To make the matter more complex and inextricable, such a whiplike flagellum has evolved parallely many times in different species in Steninae, Euaesthetinae, Aleocharinae, etc. Consequently, the copulatory tubes in Staphylinidae are difficult to homologize. And, third, it is also difficult to understand the homologous relations of the parts of a copulatory tube among the various groups of Staphylinidae.

Here, I present a detailed study of the structures and functions of the endophallic copulatory tube in the family Staphylinidae. First, I discuss the general structures of the copulatory tube and the pseudocopulatory tube, together with the characterizations and terminology. Second, the distribution of the copulatory tubes in Staphylinidae is described and briefly discussed. Third, I describe the structures of the seven basic and some other unique forms of the copulatory tubes in detail in Staphylinidae, paying special attention to those of Steninae. Fourth, I describe or hypothesize the functions of the copulatory tubes in Staphylinidae, paying special attention to those of Steninae.

13.2 Some Morphological Terms

Some morphological terms are not consistently used; and then the term (e.g., "endophallus") has several different meanings because each has been previously used differently by different authors. Thus, they are ambiguous and difficult to use in a precise way. Some other terms also are so because some morphological parts (that are designated by those terms) are complex in structure and position. In order for readers to understand the precise meanings of some important morphological terms used in this paper, I discuss here some important details.

Endophallus Following Nichols (1989: 239), the "endophallus" is described as follows: "In the male insects, the internal sac or tube of the phallus invaginated at the end of the aedeagus,. . . ." (Note here that the terminal membranous part of the aedeagus in insects has been in general called "vesica," but Sharp and Muir (1912: 585) called it "internal sac.") It seems that this characterization is incomplete. This is because, according to this characterization, the endophallus comprises of "internal sac" or "internal tube," but in many cases, it is composed of "the internal sac and tube." Namely, there exist within an aedeagus, both the internal tube (which is connected anteriorly with the reversible internal sac) and the internal sac (which is connected anteriorly with the rim of the apical foramen). Thus, I consider here that the endophallus consists of the internal structures of aedeagus containing the copulatory tube, internal sac, and its related sclerites.

Basal chamber of copulatory tube Klimaszewski (1984) and Naomi (2006a, b) called the basal swollen portion of the endophallic flagellum "sperm(a) sac," while Gack and Peschke (1994) called the inner sac of the spermatophore "sperm sac." Thus, presently, the term "sperm sac" is a homonym. The latter usage of the term "sperm sac" seems to be adequate, given that the sperm is deposited within the inner sac of a spermatophore. Thus, to avoid the terminological confusion caused by the term "sperm sac," I call the basal swollen portion of the copulatory tube "basal chamber."

Dorsal side of aedeagus In general, the dorsal side of the aedeagus in Staphylinidae is the side opposite to the parameral attachment; and thus it is sometimes called "non-parameral" or "abparameral" (Gusarov 2003: 9) side. However, in Steninae the dorsal side of the aedeagus is the upper side of the aedeagus on which the parameres are attached, because the aedeagus of Steninae is positioned in situ within the abdomen, in such a way that the parameres face dorsally. This is the reverse of the situation in many other Staphylinidae.

13.3 Endophallic Copulatory Tube and Pseudocopulatory Tube

In the taxonomic studies of staphylinids, the intromittent sclerite of the aedeagal median lobe has been called as "basal tube" (Naomi 2006a, b; Naomi et al. 2017), "copulatory piece" (Maruyama and Klimaszewski 2004; Maruyama 2008), "dorsal copulatory piece" (Brunke et al. 2016), "endophallus" (Nomura 2001a; Irmler 2005), "flagellum" (Ashe 1984, 1992), "guide sclerite" (Löbl and Calame 1996), "internal structure of male genitalia" (Hammond 1973), etc. These endophallic structures are certainly highly diverse morphologically within Staphylinidae, but due to the existence of various intermediate conditions, we can trace the morphological transformation series from the original forms (simple, short setal structures) to one extremity (very thick sticks) or to the other extremity (whiplike, very long flagella). Furthermore, as mentioned later, we can also understand that these structures basically consist of same morphological components. Thus, they are considered homologous structures from the genuine morphological point of view. Note however that all endophallic sclerites that have been previously called variously by the aforementioned terms in descriptive studies are not necessarily copulatory tubes.

First, all these intromittent sclerites are used and function during a copulation; and second, although they are highly morphologically diverse in Staphylinidae, ranging from the thick and stiff rods to the whiplike, very long, flexible flagella, they all are tubular structures. Note here that the tube is open only at the dorsal side in *Aleochara* (Gack and Peschke 2005: 309, Fig. 1C) or only at the ventral side in *Stenus* (Naomi 2006a, b), so that it is a U-shaped tube in cross section. Given the function and structure of the endophallic intromittent sclerites, they are here collectively called "copulatory tubes."

Precisely, what is the endophallic copulatory tube in Coleoptera? In order to identify the copulatory tube, we need to settle the landmark for its circumscription. The ejaculatory duct is formed by an ectodermal invagination; and the position of its opening is supposed to be settled in the early stage of genital morphogenesis (Hemming 2003). Thus, the position of the gonopore (i.e., the opening of the ejaculatory duct: Fig. 13.1a, b) can be considered an important landmark for identifying the endophallic copulatory tube in Coleoptera (see Matsumura and Yoshizawa 2012 in the case of the flagellum). By using the position of gonopore as its landmark, we will be able to characterize the coleopterous copulatory tubes. When characterizing it in an appropriate way, we must consider the following two points: first, the copulatory tube can be regarded as an endophallic tube that is distal from the opening of the ejaculatory duct; and second, the characterization must be applied to the morphologically diverse forms of the tube located at the apex of the endophallus. The copulatory tube of Coleoptera can be thus characterized as "a sclerotized, rod-, tube-, or whiplike terminal extension of the ejaculatory duct which is distally located from the opening of the ejaculatory duct (i.e., primary gonopore"; Fig. 13.1a, b) in such a way that we can regard a thick, stiff stick as well as a long, whiplike tube of the endophallus, as the copulatory tube.

A major problem here is that the endophallic copulatory tubes are highly diverse morpholog-

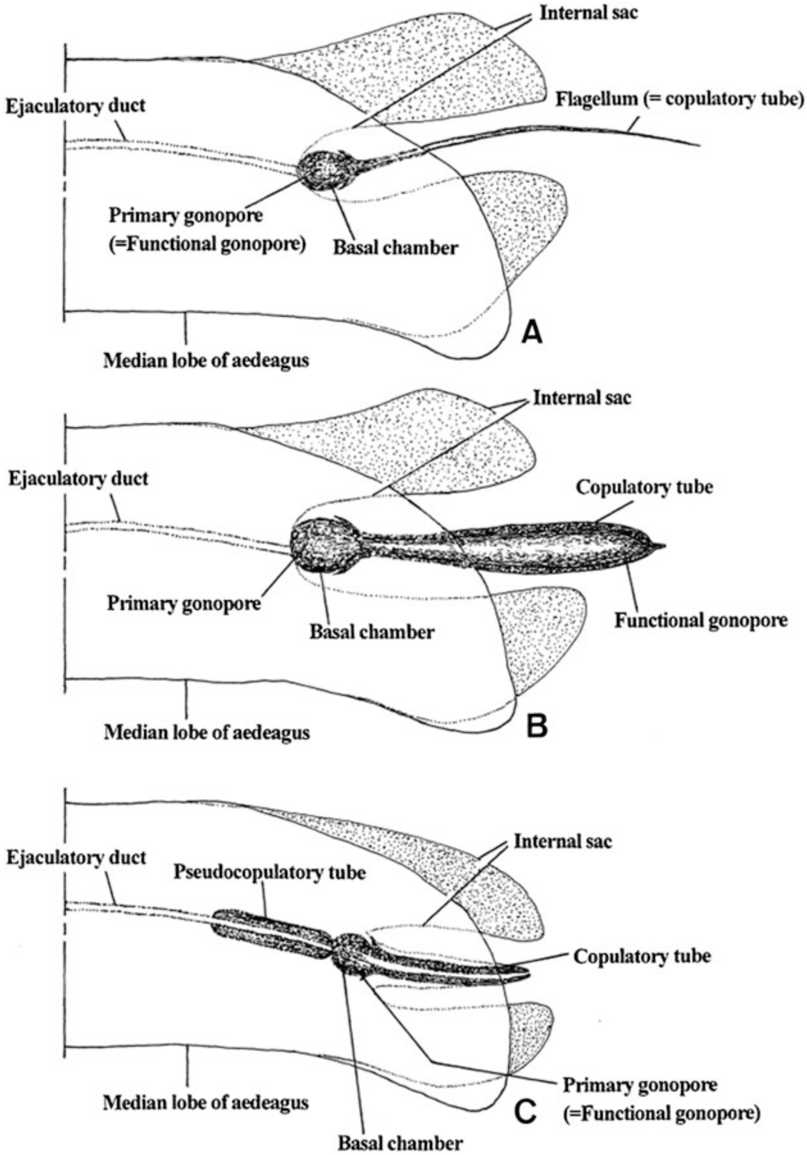

Fig. 13.1 Diagrams of the endophalli in Staphylinidae (lateral views). (**a**) Copulatory tube (= flagellum) in which the primary gonopore corresponds in place to the functional gonopore; (**b**) copulatory tube in which the primary gonopore does not correspond in place to the functional gonopore; (**c**) pseudocopulatory tube and copulatory tube

ically; and thus, coleopterists have used various descriptive terms that are suitable for the conditions of copulatory tubes that they studied. This is really the case for the “flagellum” (Fig. 13.1a), which is in some cases (e.g., Peschke 1978) called “virga” (Snodgrass 1935: 622). The endophallic flagellum of insect is characterized by Nichols (1989) as “sclerotized terminal prolongation of the ductus ejaculatorius, usually concealed within the internal sac when in repose, but sometimes very long and constantly protruding through the ostium of the penis.” The flagellum of Coleoptera is similarly described as “internal sac of a very long, slender eversible type” (Crowson 1981) or by other slightly different wordings in textbooks. I think that these traditional characterizations of the flagellum represent reasonable attempts made during the expansion of the knowledge of insect morphology; and in those senses, they can apply to the terminal, tubular, or whiplike modifications of the ejaculatory duct and thus are useful for descriptive purposes.

However, those characterizations are not precise, because we do not know, by using such wordings, how to homologize the flagellum or how to distinguish the flagellum from the ejaculatory duct. Note here that the so-called flagellum is a form of the copulatory tube; and consequently, it is the long or very long, whiplike form of the copulatory tube. The proper characterization of a flagellum may be obtained by slightly modifying the characterization of the copulatory tube as shown above. The endophallic flagellum is therefore characterized as “a whiplike, flexible terminal extension of the ejaculatory duct which is distally located from the opening of ejaculatory duct (i.e., the primary gonopore”; Fig. 13.1a). Note also that the term flagellum, by its characterization, designates the whiplike tube that includes, if present, the basal (swollen or ovoidal) chamber.

The above characterizations seem to be sufficient for identifying the endophallic copulatory tubes of Staphylinidae, but an important point is that, in the endophallus of a few Staphylinidae (e.g., some *Stenaesthetus* species), there exist another terminal sclerotizations of the ejaculatory ducts which are nonhomologous to the copulatory tubes. This endophallic sclerotization (which I call “pseudocopulatory tube” in this paper; Fig. 13.1c) is similar in structure to the true copulatory tube because it is tubular. In insects, the epithelial wall of the ejaculatory duct is surrounded by a strong muscular sheath (Snodgrass 1935: 572). Given that the position and structure of the pseudocopulatory tube is the same as in the muscular sheath, the pseudocopulatory tube may be identical with a special form of the muscular sheath, which may aid in ejaculating the sperm (enveloped in a spermatophore). It just forms the apical portion of the ejaculatory duct, but it is distinctly different from the true copulatory tube because of the following two reasons: first, the opening of the ejaculatory duct (i.e., primary gonopore) is located at its tip, but not at its base (Fig. 13.1c), and, second, it is located just proximal to the true copulatory tube (e.g., *Stenaesthetus apterus* Puthz 1988a, Fig. 6); in other words, the pseudocopulatory tube is directly connected at its most distal portion with the base of the true copulatory tube.

Since this paper strictly deals with the true copulatory tubes (but not with the various tubular structures of the endophallus including pseudocopulatory tubes), the pseudocopulatory tube should be clearly distinguished from the true copulatory tube, to correctly identify the latter in Staphylinidae.

13.4 Distribution of Endophallic Copulatory Tubes in Staphylinidae

Since, in Staphylinidae, the distribution of the species that have the aedeagus with an endophallic copulatory tube is very characteristic and interesting, I describe it here before describing and dealing with the matter of structures and functions of the copulatory tubes in Staphylinidae.

In Staphylinidae, the simple form of the endophallus is composed of a simple reversible internal sac (Fig. 13.3a); and it is often furnished (or covered) internally with spines and/or spinules (Fig. 13.3e). These primitive conditions are widely found in many groups of staphylinids including *Cerapeplus* (Löbl and Burckhardt 1988), *Dasycerus* (Löbl and Calame 1996), *Glypholoma* (Thayer and Newton 1978; Thayer 1997), *Neophonus* (Thayer 1987), *Habrocerus* and *Nomimocerus* (Assing and Wunderle 1995), *Pseudopsis* (Herman 1975), *Trichophya* (Ashe and Newton 1993), *Xantholinus* (Bordoni 2002, 2011), etc. The endophallic copulatory tube is not found in the aedeagus of these staphylinids.

However, the species that have the aedeagus with a copulatory tube are widely scattered in the various subfamilies of Staphylinidae (Table 13.1): omaliine group (Omaliinae, Proteininae, Dasycerinae, Pselaphinae); oxyteline group (Trigonurinae, Oxytelinae, Osoriinae, Scaphidiinae); tachyporine group (Tachyporinae, Phloeocharinae, Aleocharinae), and staphylinine group (Oxyporinae, Paederinae, Staphylininae, Scydmaeninae, Megalopsidiinae, Euaesthetinae, Steninae, Leptotyphlinae). Major characteristics regarding the distribution of the copulatory tubes in Staphylinidae are as follows:

1. The copulatory tubes are found in both, the basal subfamilies (e.g., Trigonurinae, Omaliinae, Tachyporinae, Oxyporinae) and more advanced ones (e.g., Pselaphinae, Aleocharinae, Euaesthetinae, Steninae, Leptotyphlinae). However, the subfamilies with many component species having the aedeagus with a copulatory tube belong to the evolutionally advanced subfamilies (i.e., Pselaphinae, Aleocharinae, Euaesthetinae, Steninae, Leptotyphlinae). As far as I know, there is no staphylinid subfamily, with all species having the aedeagus with a copulatory tube.
2. The distribution of the species with a copulatory tube in a given subfamily (in which species with a copulatory tube are found) is rather biased; that is, the copulatory tube is in general restrictedly found in the species of some particular groups of the subfamily. For example, in Paederinae, the copulatory tube is found in many species of *Scopaeus* (Frisch 1997, 1998, 1999, 2003). In Aleocharinae, the copulatory tube/flagellum is found in many species of Gyrophaenina (Ashe 1984), Bolitocharina (Ashe 1992), Aleocharini (Klimaszewski 1984; Yamamoto and Maruyama 2012), etc. In Staphylininae, the copulatory tube is found in many species of Othiini (Assing 1999) and *Cyrtoquediina* (Brunke et al. 2016).
3. In small-sized genera, only one or several species have the aedeagus with a copulatory tube. For example, out of 17 worldwide species of *Dasycerus*, only one species *D. angulicollis* has the copulatory tube (Löbl and Calame 1996) among the large genera. The genus *Ocypus* seems to be also an example of this. Out of 56 species of the genus *Ocypus* distributed in the west part of Palaearctic region, only one species *O. similis* possesses the aedeagus with a copulatory tube (Coiffait 1974).
4. When many species of a genus possess the copulatory tube, then various forms of the copulatory tube are found within the genus under consideration. This is, for example, true for *Stenus* and *Dianous* (Table 13.1).

13.5 Structures of Endophallic Copulatory Tubes in Staphylinidae

13.5.1 General Structure of the Copulatory Tube

In Staphylinidae, the endophallic copulatory tube is in general composed of a basal chamber and a main tube (Fig. 13.2). The basal chamber is very small to moderate or large in size; and it is usually ovoidal or fusiform when it is swollen. It is, however, often missing (e.g., *Kathetopodion*, Leschen and Löbl 2005). If present, the basal chamber is usually demarcated by a basal constriction from the main tube (Fig. 13.2). The main tube is very often divided into two components: the basal tube and the apical tube (Fig. 13.2); in other words, the copulatory tube is tripartite (basal chamber, basal tube, and apical tube) in such cases. The copulatory tube is easily distinguishable from the ejaculatory duct in many cases,

Table 13.1 Representatives of the higher taxa of Staphylinidae, in which the species with an endophallic copulatory tube are included

Aleocharinae[a]: *Adelarthra* [4]: Ashe (2003); *Aleochara* [3v, 4]: Gack and Peschke (1994, 2005), Yamamoto and Maruyama (2012); *Aphaenochara* [3v]: Maruyama and Hlavác (2003); *Aspidobactrus* [2ra]: Maruyama (2000); *Autalia* [4]: Hoebeke and Ashe (1994); *Baeosthethus* [2v]: Steel (1964); Bolitocharina [2ra, 2rb, 3v]: Ashe (1992); *Creochara* [4]: Maruyama (2004a); *Diaulota* [1r, 2ra]: Ahn (1996); *Dinusa* [2v]: Assing (2001); *Giraffaenictus* [2rb]: Maruyama (2008); *Goniusa* [2ra]: Maruyama and Klimaszewski (2004); Gyrophaenina [2ra, 3v, 4, 5]: Ashe (1984); *Halorhadinus* [2ra, 2rb]: Ahn (2001); *Hygropetrophila* [4]: Wunderle and Assing (2000); *Kistnerella* [4]: Kanao et al. (2011); *Leptusa* [2ra, 2rb, 3, 4]: Pace (1999), Smetana (1973); *Liparocephalus* [2rb]: Ahn (1997); *Myllaena* [4]: Pace (2009); *Myrmecopella* [2ra, 3]: Maruyama (2004b); *Myrmecosticta* [4]: Maruyama et al. (2011); *Oligota* [2ra, 2rb, 3v, 4]: Williams (1976, 1978); *Oreokklina* [2ra]: Assing (2002); *Orphnebius* [2rb]: Assing (2006); *Oxypoda* [2ra, 2rb, 3, 4]: Pace (2010), Assing (2012); *Pella* [1r, 2rb]: Maruyama (2006); *Phanerota* [3, 4]: Ashe (1986); *Rothium* [2rb, 3v]: Ahn and Ashe (1996); *Tetrasticta* [4]: Maruyama and Sugaya (2002); *Zoosetha* [2rb]: Assing (2003)
Dasycerinae: *Dasycerus* [2v]: Löbl and Calame (1996)
Euaesthetinae[b]: *Edaphosoma* [2ra, 2rb, 3v]: Puthz (1986a, 2010); *Edaphus* [2ra, 2rb, 3, 4]: Puthz (1985a, 1986b, 1992); *Euaesthetus* [2ra, 2rb, 3, 3v, 4, 5, 6]: Puthz (1998, 2014); *Kiwiaesthetus* [2ra]: Puthz (2008b); *Nothoesthetus* [2rb]: Puthz (2012b); *Octavius* [2ra, 3, 3v, 4, 6]: Puthz (1977, 1985b, 1986c, 1989c); *Orosthetus* [4]: Puthz (1979); *Schatzmayrina* [3, 3v, 4]: Puthz (1978, 1989a); *Stenaesthetus* [2rb, 2v, 4]: Puthz (1988a, 2011a); *Stictocranius* [3v, 4]: Puthz (1989b, 2011b); *Tamotus* [2rb, 3]: Puthz (1973, 2002); *Turellus* [3, 4]: Puthz (1974, 1976)
Leptotyphlinae: *Cyrtotyphlus* [3v]: Coiffait (1972); *Entomoculia* [3, 3v, 6]: Coiffait (1972); *Mesotyphlus* [2ra, 3, 6]: Coiffait (1972); *Paratyphlus* [2ra, 2v]: Coiffait (1972); *Hesperotyphlus* [5, 6]: Coiffait (1972)
Megalopsidiinae: *Megalopinus* [2v, 3v, 5, 6]: Puthz (2012a, c)
Omaliinae: *Eusphalerum* [1r, 2ra, 2rb]: Zanetti (2014); *Geodromicus* [3v, 4]: Shavrin (2012)
Osoriinae: *Allotrochus* [3]: Naomi and Irmler (2012); *Apotocnemius* [3v]: Naomi (1986); *Holotrochus* [3v, 4]: Irmler (1981, 2005); *Lispinus* [4]: Naomi (1996); *Nacaeus* [4]: Naomi (1997a); *Osorius* [3v, 4]: Naomi (1986); *Thoracophorus* [4]: Irmler (1985)
Oxytelinae: *Thinobius* [1r, 2rb]: Makranczy and Schülke (2001)
Oxyporinae: *Oxyporus* [2ra]: Hwang and Ahn (2000)
Paederinae: *Acaratopus* [4]: Herman (1981); *Micrillus* [3v, 4]: Assing (2013); *Pinobius* [3, 3v, 4]: Assing (2014); *Pinophilus* [4]: Abarbanell and Ashe (1989); *Scopaeus* [2ra, 2rb, 3, 4]: Frisch (1997, 1998, 1999, 2003)
Phloeocharinae: *Charhyphus* [4]: Herman (1972)
Proteininae: *Nesoneus* [4]: Steel (1966); *Paranesoneus* [4]: Steel (1966)
Pselaphinae: *Articerodes* [2ra]: Nomura (2001b); Batrisina [3, 3v, 5, 6]: Nomura (1991); *Megatyrus* [3v, 5]: Nomura et al. (2011); *Octomicrus* [6]: Nomura (2010); *Odontalgus* [6]: Arai and Nomura (2003); *Paralasinus* [3v, 5]: Hlaváč and Nomura (2001); *Pselaphogenius* [5, 6]: Nomura (2001a)
Scaphidiinae: *Baeocera* [1r, 2ra, 3, 4]: Löbl (2012, 2015); *Bertiscapha* [2v, 3v]: Leschen and Löbl (2005); *Kathetopodion* [1sa]: Leschen and Löbl (2005); *Scaphisoma* [1r, 2ra, 3v, 4]: Löbl (2002, 2015); *Xotidium* [3v, 4]: Ogawa and Löbl (2016)
Scydmaeninae: *Cephennodes* [2ra, 3, 3v]: Jałoszyński and Nomura (2009); *Cephennomicrus* [1r]: Jałoszyński (2010); *Hlavaciellus* [2ra]: Jałoszyński (2010)
Staphylininae: *Ocypus* [4]: Coiffait (1974); *Othius* [4]: Assing (1999); *Xantholinus* [1sa, 1sb, 2s]: Coiffait (1972)
Steninae[c]: *Stenus*: [2ra, 2rb, 3, 3v, 4, 5, 6, 7]: Puthz (2000b, c, 2003b, 2008a, 2013), Naomi (2006a, b); *Dianous* [2ra, 2rb, 3, 3v, 4, 5, 6, 7]: Puthz (1988b, 2000a)
Tachyporinae: *Ischnosoma* [1r, 2ra, 2rb]: Kocian (1996); *Sepedophilus* [2rb, 3, 4]: Hammond (1973), Naomi and Maruyama (1998); *Tachinus* [1r, 2ra]: Kim and Ahn (2000)
Trigonurinae: *Trigonurus* [3v]: Kishimoto (2000)

[1r], [1s], [2ra], [2rb], [2s], [2v], [3], [3v], [4], [5], [6], and [7] mean the form 1r, form 1s, form 2ra, form 2rb, form 2s, form 2 (variation), form 3, form 3 (variation), form 4, form 5, form 6, and form 7 of copulatory tube, respectively. The numbers refer to those shown in Figs. 13.3 and 13.4

[a]A characteristic of the Aleocharinae copulatory tube is that the apical part of the main tube sometimes strongly curves (e.g., *Bolitochara*: Ashe 1992; *Myrmecopella*; Maruyama 2004b). Another characteristic is that the flagellum goes out from the median lobe at its dorso-basal part (e.g., *Adelarthra*: Ashe 2003; *Sternotropa*, *Pseudoligota*: Ashe 1984) or at its ventro-basal part (e.g., *Pseudoligota*: Ashe 1984) when it is longer than the whole length of the aedeagus

[b]The structure of the copulatory tube is highly diverse in Euaesthetinae; and there are found various forms including the very thin, extremely long flagella (form 4) and thick, sticklike tubes (forms 5 and 6)

[c]The structure of the copulatory tube is highly diverse in Steninae (forms 2–7), as in Euaesthetinae. The Euaesthetinae and Steninae are presently considered to have the sister-group relationship (Clarke and Grebennikov 2009; Mckenna et al. 2015), and thus the highly morphological diversity of the endophallus seems to be a characteristic of the clade comprising the Euaesthetinae and Steninae

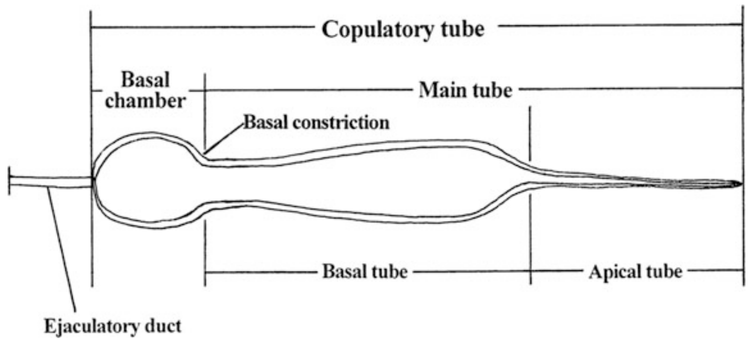

Fig. 13.2 Diagram of the general structure of the copulatory tube in Staphylinidae

because the base of copulatory tube (i.e., the basal chamber) is more or less swollen (Fig. 13.2). Even in cases of the copulatory tube without a basal chamber (e.g., *Pinophilus*; Abarbanell and Ashe 1989), it may be easily distinguishable from the ejaculatory duct in most cases, because the proximal portion of the copulatory tube is more or less thick than the ejaculatory duct.

In the copulatory tube of Staphylinidae (Fig. 13.1a, b), the opening of the ejaculatory duct (first gonopore) is not necessarily identical with the opening, through which the spermatophore (or sperm) is ejaculated during copulation (second gonopore). In some species of staphylinids, the first gonopore seems to substantially correspond in its position to the second (Fig. 13.1a). Namely, the first gonopore is located at the bottom of the basal chamber, and it is through this opening that the spermatophore (or sperm) is transferred to the vagina during copulation (e.g., *Aleochara*; Gack and Pescke 1994). However, in some other species of Staphylinidae, the first gonopore does not correspond in position to the second (Fig. 13.1b). Namely, the first gonopore is located at the bottom of the basal chamber, whereas the second is at the middle of the copulatory tube or at or near its tip (e.g., some *Stenus*: Fig. 13.6g; Naomi 2006b). Thus, these two openings should be precisely distinguished in the morphological studies of Staphylinidae. In this paper, the first gonopore is termed "primary gonopore," whereas the second one is termed "functional gonopore."

13.5.2 Seven Basic and Some Other Unique Forms of Copulatory Tubes

The endophallic copulatory tubes are highly morphologically diverse in Staphylinidae, as mentioned above, but they seem to be basically classified into seven forms. In this subsection, the structures of these seven basic forms are first described in detail; and then some other unique forms of the copulatory tubes are described.

13.5.2.1 Form 1 (or Original Form) of Copulatory Tube

Concerning the original forms of the copulatory tube in Staphylinidae, empirical data suggest that there seems to be two candidates. First, a simple bulbous chamber (Fig. 13.3b) should be considered an original form of a copulatory tube, because it is an extension of the ejaculatory duct which is distal to the primary gonopore. It consists only of the basal chamber; and it is here regarded as "form 1r." It is found in some *Thinobius* (Makranczy and Schülke 2001), etc. Second, a simple, seta-like sclerite (Fig. 13.3f, g) is also regarded as the other original form of a copulatory tube ("form 1s"). It consists of the simple main tube (i.e., a seta-like sclerite), with (Fig. 13.3f) or without (Fig. 13.3g) setulae around it. These two are here regarded as "form 1sa" and "form 1sb," respectively. The form 1s is found in the endophallus which is covered densely with spines and spinules. It is rare in Staphylinidae; and it occurs in some *Xantholinus* (Coiffait 1972:

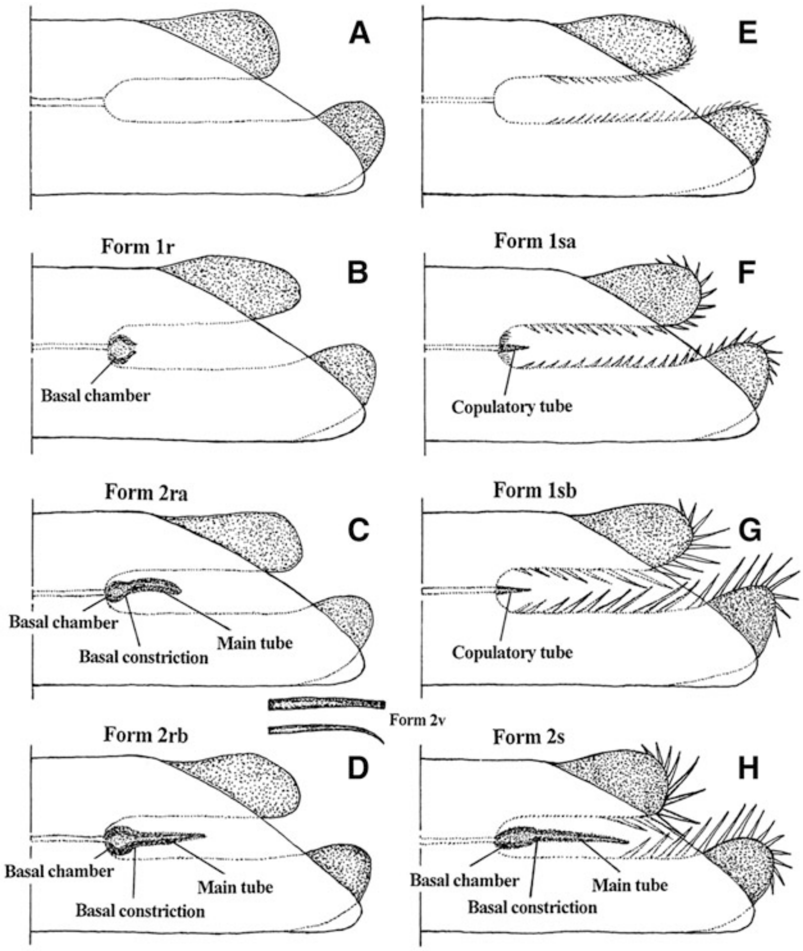

Fig. 13.3 Diagrams of the endophalli in Staphylinidae (lateral views). (**a**) Internal sac without modification; (**b**) internal sac with the copulatory tube (form 1r); (**c**) internal sac with the copulatory tube (form 2ra); (**d**) internal sac with the copulatory tube (form 2rb); (**e**) internal sac with setulae; (**f**) internal sac with the setulae and copulatory tube (form 1sa); (**g**) internal sac with the setae and copulatory tube (form 1sb); (**h**) internal sac with the setae and copulatory tube (form 2s)

241) and some Scaphidiines (Leschen and Löbl 2005: 34).

13.5.2.2 Form 2 of Copulatory Tube ("Copulatory Piece Auctorum")

The form 2 of a copulatory tube is composed of the basal chamber and a simple main tube (Fig. 13.3c, d, h). The basal chamber is small (Fig. 13.3c), medium (Fig. 13.3d, h), or large in size (e.g., some *Diaulota*; Ahn 1996). The basal constriction is indistinct (Fig. 13.3c, h) or distinct (Fig. 13.3d). The main tube is basically short and thin or moderately thick; it simply tapers toward the pointed apex (Fig. 13.3d, h) or is more or less curved (Fig. 13.3c). There often exist variations of form 2. They vary in structure, namely, they are thin to moderately thick, short to moderately long, and straight or curved, but they do not have a basal chamber (e.g., *Dasycerus*: Löbl and Calame 1996). They are classified into the "form 2v" in Fig. 13.3 and Table 13.1. The form 2 (and also 3) are rather different in structure from the typical whiplike flagellum and also from the thick, sticklike tube;

and they have been called by various terms (e.g., "copulatory piece," "guide sclerite," and "endophallus") in descriptive studies.

The form 2 of the copulatory tube is common in Staphylinidae (Table 13.1), but it is considered that the origins of these copulatory tubes must be different, because there are two different original forms described above. The "form 2ra" (Fig. 13.3c) and "form 2rb" (Fig. 13.3d) are here considered as derived from the form 1r, by extending posteriorly the distal portion of basal chamber. The "form 2s" (Fig. 13.3h) and its variations are here considered as derived from the form 1sa or 1sb, by enlarging its base and extending the main tube posteriorly (e.g., *Xantholinus linearis*; Coiffait 1972: 236). The form 2s and its variations are found in the endophallus which is covered densely with spines and spinules (e.g., in Xantholinine genera; Bordoni 2002, 2011; Coiffait 1972). (Note here that once a copulatory tube has evolved into the form 3 or other advanced forms (i.e., whiplike form 4 and thick forms 5–7), we cannot see in general whether the copulatory tube is derived from a simple seta-like sclerite or from a simple basal chamber.)

13.5.2.3 Form 3 of Copulatory Tube ("Copulatory Piece Auctorum")

The form 3 of the copulatory tube is in general tripartite; and it is composed of the basal chamber and the main tube (basal tube + apical tube) (Figs. 13.4 and 13.5c–e). It is basically long; and it is sometimes a little shorter than the whole length of the aedeagus. The proximal part of the copulatory tube is swollen to form a basal chamber; and when seen from the ventral side, it consists of "two thin rods" in some *Stenus* (Naomi 2006a, b). The main tube is U-shaped in cross section; and the basal tube is thin (Fig. 13.5c, d) or moderately thick (Fig. 13.5e), while the apical tube is whiplike (Fig. 13.5c) or moderately thick (Fig. 13.5e). The main tube is almost straight (Fig. 13.5c) or weakly (Fig. 13.5d) or strongly curved, but it basically tapers apically, and the demarcation between the basal tube and apical tube is indistinct.

There are variations of form 3. The "form 3v" is slightly different from the typical form 3 (Figs. 13.4 and 13.5e). For example, in some cases, the main tube is hardly divided into the basal and apical tubes (Fig. 13.5c, d); or it is

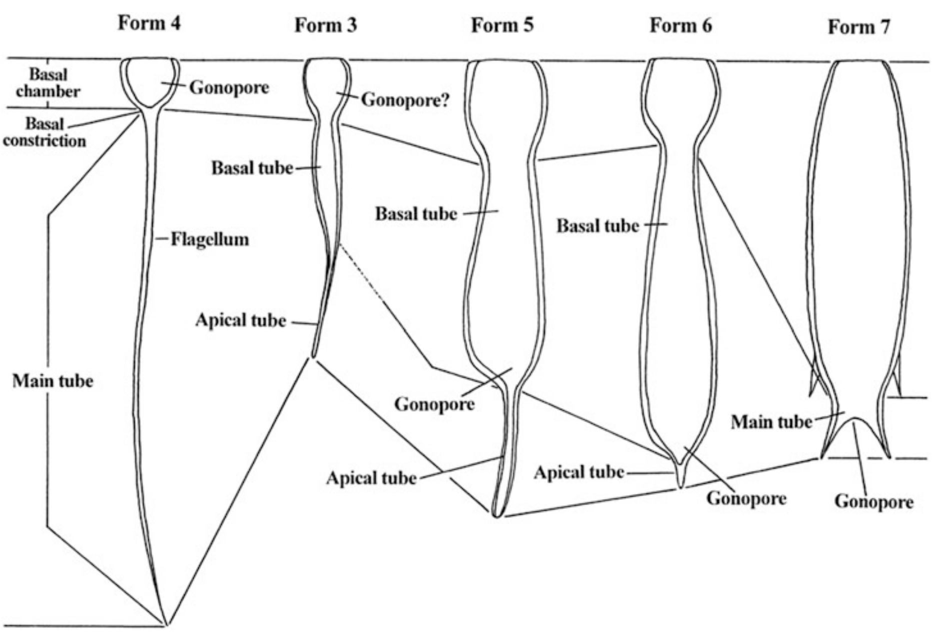

Fig. 13.4 Diagrams of the endophallic copulatory tubes (forms 3–7) in Staphylinidae. The lines are drawn, which show homologous parts of the different forms of the copulatory tubes

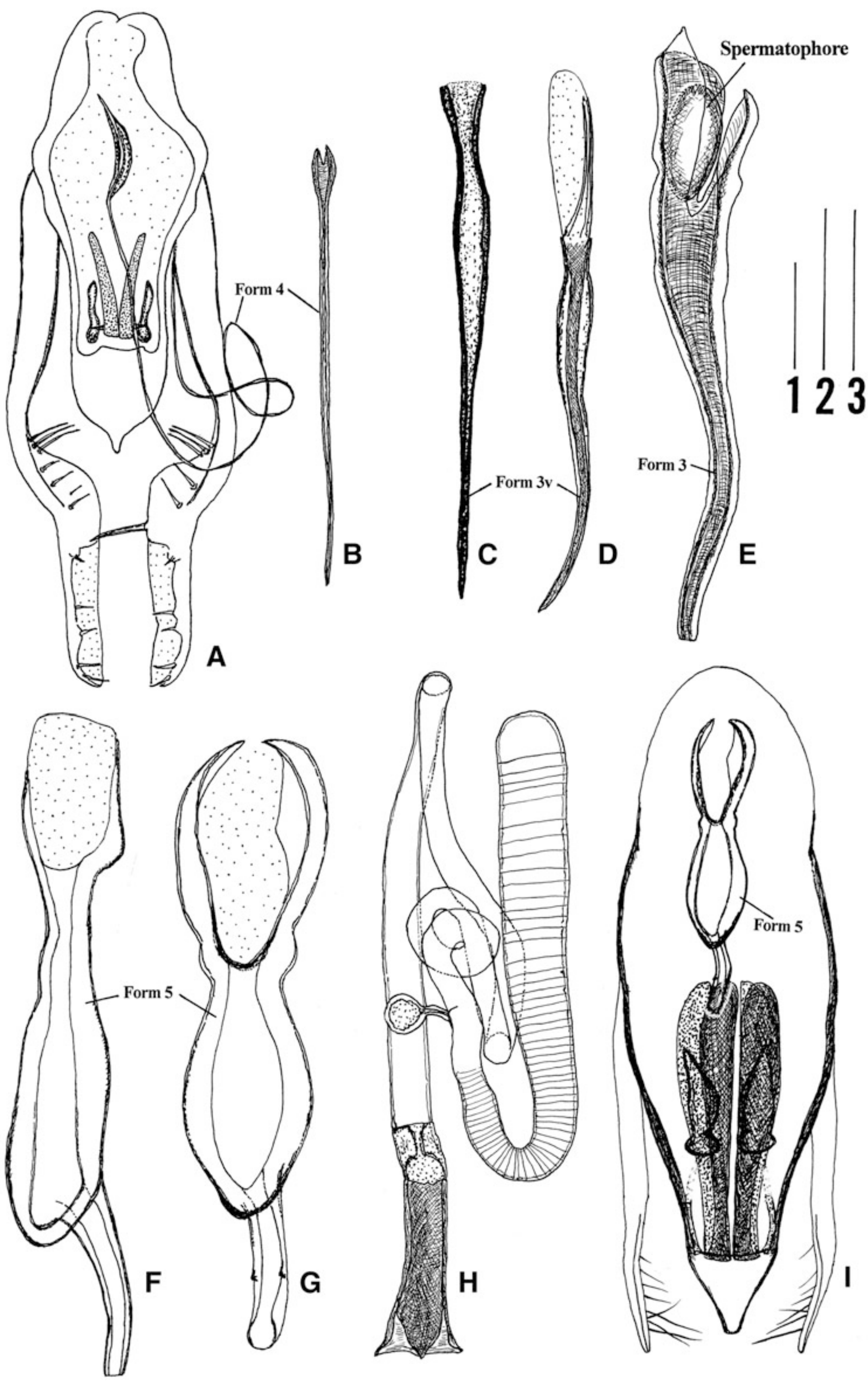

Fig. 13.5 (**a**, **i**) Aedeagi (ventral view); (**b**–**g**) copulatory tubes (ventral view); (**h**) spermatheca. (**a**) *Stenus riukiuensis* Puthz; (**b**) *S. miroku* Naomi; (**c**) *S. unagi* Hromádka; (**d**) *S. gagyumontis* Naomi; (**e**) *S. ohtoensis* Naomi; (**f**) *S. olliformis* Naomi; (**g**)–(**i**) *S. ebisu* Naomi (**a**, **c**: original illustration; **b**, **d**–**i**: Naomi 2006b) Scale 1: 0.1 mm for (**a**); scale 2: 0.1 mm for (**b**)–(**h**); scale 3: 0.2 mm for (**i**)

entirely sticklike so that it has the same or similar thickness from the base to the apex. The basal chamber is missing in some other cases. In cases where a copulatory tube is thin, moderately long, and weakly tapers apically (e.g., *Aphaenochara*; Maruyama and Hlavác 2003), the copulatory tube may be still regarded as a variation of form 3, but due to the various intermediate conditions, it is sometimes difficult to separate the form 3 from the form 2 or 4. The form 3 and its variations are, as in the form 2, common in Staphylinidae (Table 13.1).

13.5.2.4 Form 4 of Copulatory Tube ("Flagellum Auctorum")

The form 4 of the copulatory tube has been called "flagellum" in descriptive studies because it is whiplike. It consists of the basal chamber and the main tube (Fig. 13.4). The proximal part of the flagellum is more or less swollen (Klimaszewski 1984; Gack and Peschke 2005: 309, Fig. 1A: bf; Naomi 2006a, b) to form a basal chamber. The main tube is thin (Fig. 13.5b) to very thin (Fig. 13.5a), moderately long (Fig. 13.5b) to very long (Fig. 13.5a), straight (Fig. 13.5b), weakly or strongly curved, or irregularly, loosely coiled several times (Fig. 13.5a). In rare cases (e.g., *Othius bhutanensis*: Assing 1999; *Aleochara tristis*: Gack and Peschke 2005; *Stenaesthetus afer*: Puthz 2011a), it is very thin, extremely long, and regularly coiled many times. The tube is almost even in thickness from the base to the apex (Fig. 13.5a), or it weakly becomes thinner toward the apex (Fig. 13.5b). A unique flagellum is found in *Stenus paludivagus* Puthz 2000b. It is very long, wide, flat, and loosely coiled many times; and furthermore, it gradually widens toward the apex (Puthz 2000b). The form 4 is sporadically found in some species and genera of Aleocharinae, Euaesthetinae, Steninae, Othiini, etc. (Table 13.1).

13.5.2.5 Form 5 of Copulatory Tube

The form 5 of a copulatory tube is tripartite; and it is composed of the basal chamber and the main tube (basal tube + apical tube) (Fig. 13.4). Forms 3 and 5 are relatively similar in structure and thus sometimes difficult to distinguish from each other, but in the form 5 (Fig. 13.4), the basal tube is much thicker, and the basal and the apical tubes are in general easily distinguishable by a more or less distinct constriction between them. The basal chamber is small to large (Fig. 13.5f) or very large (Fig. 13.5g). The basal tube is thick (Fig. 13.5f) to very thick (Fig. 13.5g) and short to moderately long (Fig. 13.5f, g); and the apical tube is thin to feebly thick (Fig. 13.5f, g), feebly tapers toward its tip (Fig. 13.5f), or has almost the same thickness (Fig. 13.5g). The form 5 and its variations are most frequently found in Steninae, often in Pselaphinae, and in some genera of Euaesthetinae and Leptotyphlinae, etc. (Table 13.1).

13.5.2.6 Form 6 of Copulatory Tube

The form 6 of a copulatory tube consists of the basal chamber and the main tube (Fig. 13.4). Forms 5 and 6 are difficult to classify in some cases, but in the form 6, the apical tube is reduced into a small apicomedian protuberance. The basal chamber is medium to large (Fig. 13.6g) or very large sized (Fig. 13.6a, e). The basal tube is thick (Fig. 13.6a, 8) to very thick (Fig. 13.6d, e) and short to moderately long (Fig. 13.6f) or long (Fig. 13.6c). The apicomedian protuberance is small, thin, and simply pointed (Fig. 13.6a, e, g) or minutely bifurcate (Fig. 13.6d); and it is single (Fig. 13.6a, e, g) or rarely double (Fig. 13.6d). The form 6 is found in Pselaphinae, Steninae, Euaesthetinae, etc. (Table 13.1).

13.5.2.7 Form 7 of Copulatory Tube

The form 7 of a copulatory tube consists of the basal chamber and the main tube (Fig. 13.4). The basal chamber is in general stout and large (Fig. 13.6h) to very large (Fig. 13.6i). In some cases, it is modified with very thin, apicolateral projections (Fig. 13.6i), and/or others. The main tube is moderately thick (Fig. 13.6i) to thick or very thick (Fig. 13.6h) and large (Fig. 13.6h) or very large (some *Stenus*; Naomi 2010); and it usually lacks the constriction between the basal and the apical tube. It is sometimes reduced into a short and small tube or rod (Fig. 13.6i). The main tube has accessory lobes, protuberances, etc. in some cases. For example,

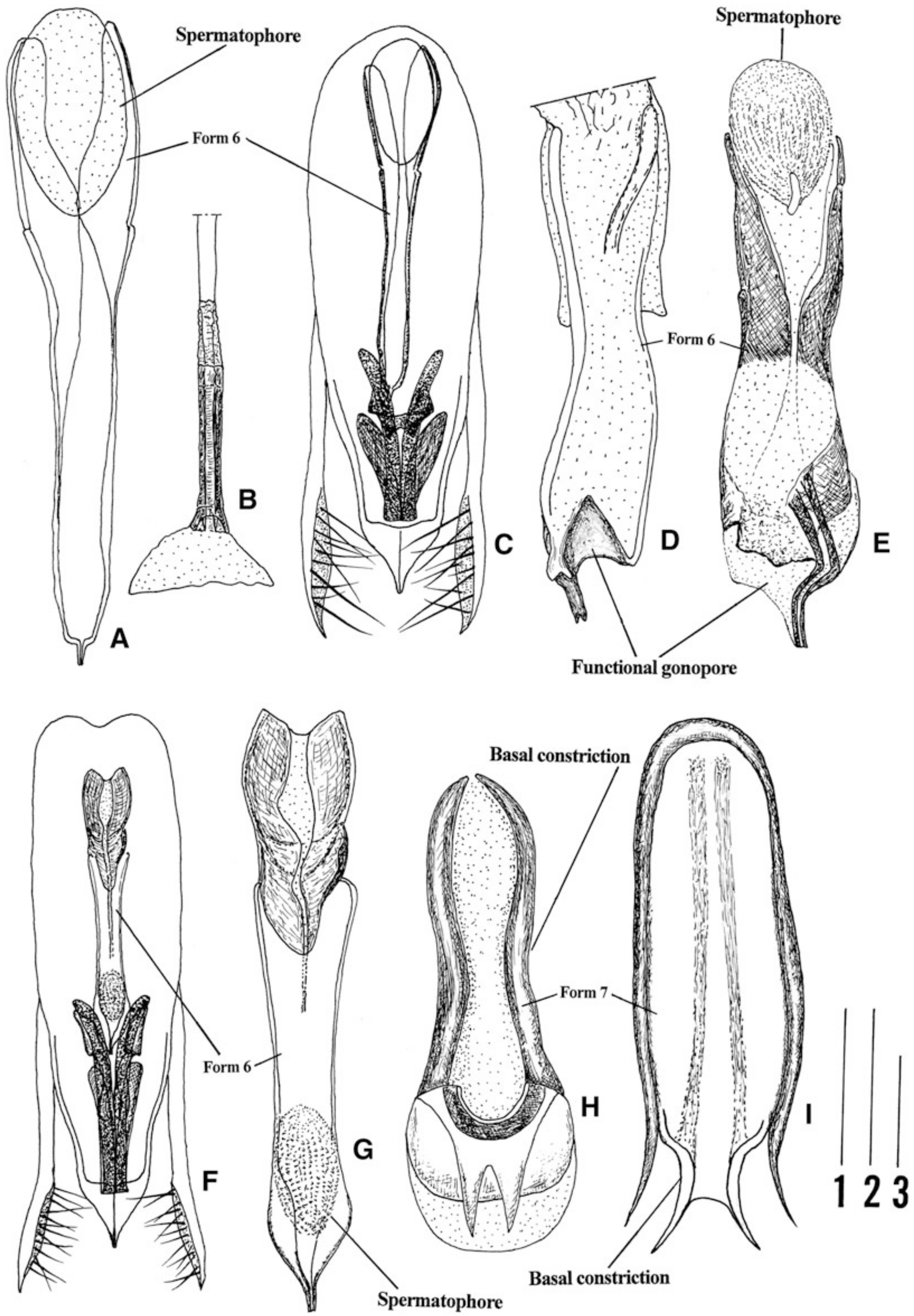

Fig. 13.6 (**a**, **d**, **e**, **g–i**) Copulatory tubes; (**b**) basal portion of spermatheca; (**c**, **f**) aedeagi in ventral view. (**a**)–(**c**) *Stenus ichihashii* Naomi; (**d**, **e**) *S. nakanei* Hromádka; (**f**, **g**) *S. gyrosus* Naomi; (**h**) *S. yasuhikoiellus* Naomi; (**i**) *Dianous coeruleovestitus* Puthz (**a–c**, **e–g**: Naomi 2006b; **d**: Naomi 1997b; **h**: Naomi 2010; **i**: original illustration) Scale 1: 0.1 mm for (**a**, **b**, **d**, **e**, **g**, **h**); scale 2: 0.2 mm for (**c**, **f**); scale 3: 0.1 mm for (**i**)

in *Stenus yasuhikoiellus*, the main tube has ventrally a deeply bifurcate lobe (Fig. 13.6h); and in *Dianous coeruleovestitus*, it has a pair of pointed lateral projections (Fig. 13.6i). The form 7 is, as far as I know, found only in Steninae.

13.5.2.8 Other Forms of Copulatory Tube

There certainly exist some other unique forms of copulatory tubes in Staphylinidae. Some representatives of the unique forms are as follows:

Corkscrew Form The copulatory tube is strongly, tightly coiled in some *Holotrochus* (Irmler 1981, 2005); and in some *Scaphobaeocera* (Hoshina and Sugaya 2003; Löbl 2015), it is thin and very loosely coined like a corkscrew. In some *Octavius* (Puthz 1989c), the copulatory tube is long and moderately thick; and just like a corkscrew, the tube is strongly, tightly coiled at least in its basal half, although the entire tube is almost straight. In some *Brachida* (Ashe 1984), the basal part of the main tube is thick and strongly, tightly coiled.

Bifurcate Form In some *Octavius* (Puthz 1977), the copulatory tube is long and moderately thick, with the apical half of main tube split longitudinally; the right lobe is thicker than the left one, and the mesial margin of the right lobe is furnished with an irregular line of 4, 5, 6, or 7 denticles. In *Cyrtoquedius* (Brunke et al. 2016) and *Euplectus lapponicus* (Löbl and Mattila 2010), the apical part of the main tube is split longitudinally.

Deformed Form In Pselaphinae (e.g., Jeannel 1959; Nomura 1991), the copulatory tube is often morphologically highly deformed, for example, in *Pselaphogenius* (Nomura 2001b) and *Octomicrus* (Nomura 2010), the main tube branches with spine-like lobes of various forms; and it is spatulate, strongly curved, asymmetric and/or sinuous. However, even in these cases, the copulatory tube yet retains some basic characteristics. Namely, it is rodlike at least at its base; and the cross section of the tube is U-shaped at least at its base.

13.6 Functions of Endophallic Copulatory Tubes in Staphylinidae

The status quo is that the functions of the endophallic copulatory tube are not studied in most groups of Staphylinidae. However, the function of the copulatory tube in *Aleochara* (as "extension tube guiding rod") was unraveled by Gack and Peschke (1994, 2005), whereas in some *Stenus*, the other function (as "spermatophore or sperm depositor") was inferred from the information obtained during my morphological studies by discovering that the spermatophores were retained in the male copulatory tube (Figs. 13.5e and 13.6e, g) and also a spermatophore was found in the female genital chamber, which was probably pasted by a male during copulation (Fig. 13.7; Naomi 2006b). Therefore, based on the present observations and descriptions of the copulatory tubes, together with available information from the published papers, it is certainly possible to reasonably hypothesize the functions of the copulatory tubes in many cases of Staphylinidae. Thus, in this section, the functions of the seven forms of the copulatory tubes are separately described and discussed. I hope that the descriptions, observations, and possible hypotheses about them in this section are not only useful for descriptive studies of Staphylinidae but also form a discussion basis for further morphological studies on them.

In this section, the term "gonopore" means the "functional gonopore" (but not the "primary gonopore"), because the position of the functional gonopore (Fig. 13.1a, b) is more useful for efficiently classifying the various forms of staphylinid copulatory tubes.

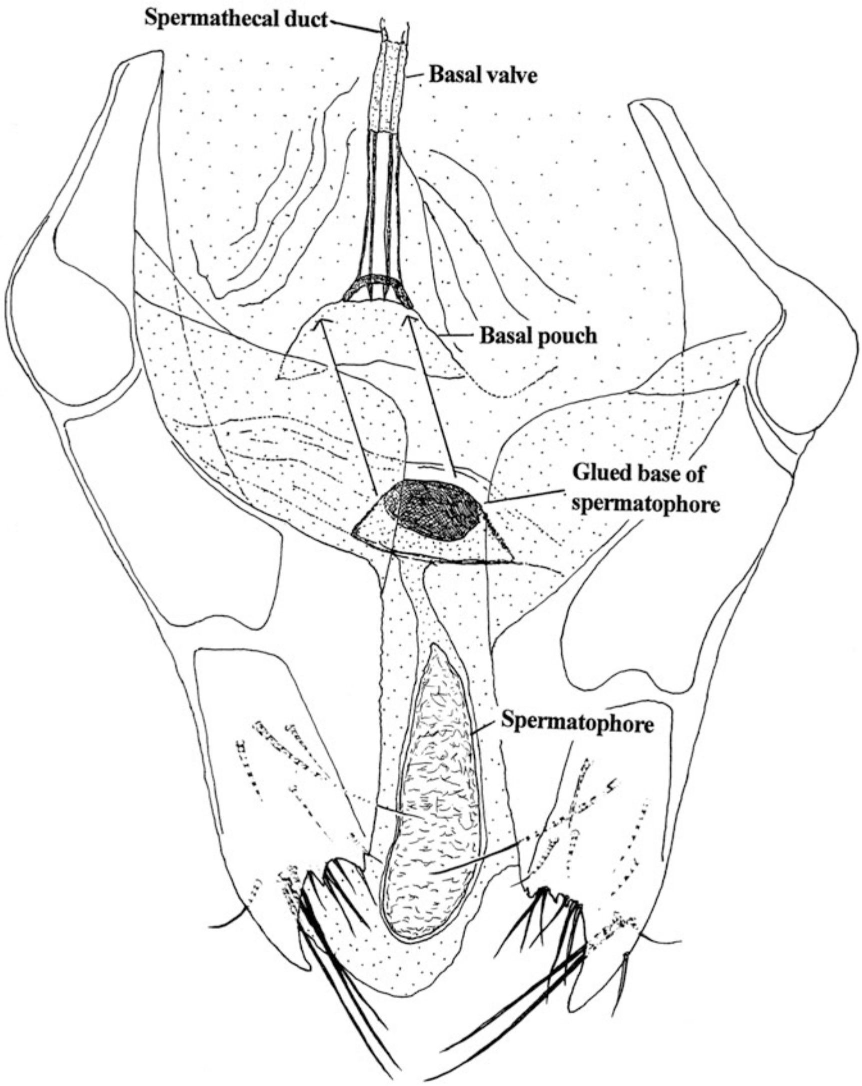

Fig. 13.7 Gonocoxites and the basal part of the spermatheca, with a spermatophore deposited in the vagina by a male (ventral view). Note that the spermatophore (which was once pasted to the basal pouch of the spermatheca by a male) comes out from the basal pouch. *Stenus ichihashii* Naomi (2006a). Scale: 0.1 mm

13.6.1 Functions of the Seven Forms of Copulatory Tubes

13.6.1.1 Form 1 (or Original Form) of Copulatory Tube

Regarding the form 1r (Fig. 13.3b), the gonopore is located at the base of the basal chamber, which functions as a chamber for storing a spermatophore (or sperms). Given its bulbous structure, the copulatory tube is supposed to play a role as a "spermatophore (or sperm) depositor" (see "form 6" of this subsection with respect to its characterization). Regarding the form 1sa and 1sb (Fig. 13.3f, g), the gonopore is supposed to be located at or near the base of the seta-like sclerite. Given its thin structure, it must function as an intromittent organ, which is inserted into the basal portion of the spermathecal duct during copulation.

13.6.1.2 Form 2 of Copulatory Tube ("Copulatory Piece Auctorum")

In the form 2 (2ra, 2rb, 2s) (Fig. 13.3c, d, h), the gonopore is located at the base of the basal chamber. In cases where the copulatory tube has a thin, attenuate main tube (2rb, 2s), it is supposed to be inserted into the spermathecal duct during copulation. However, the function of the form 2ra with the relatively thick main tube is unclear.

13.6.1.3 Form 3 of Copulatory Tube ("Copulatory Piece Auctorum")

The apical tube is whiplike so that it is too thin to transmit a large spermatophore to its tip (Fig. 13.5c, d); and thus, the gonopore is supposed to be located at or near the base of the copulatory tube. Since the whiplike apical tube is obviously thinner than the basal part of the spermathecal duct of female in some *Stenus* species (Naomi 2006a, b), the apical tube seems to have a role as an intromittent organ, which is inserted into the spermathecal duct during copulation.

13.6.1.4 Form 4 of Copulatory Tube ("Flagellum Auctorum")

The function of the form 4 (i.e., the flagellum) of *Aleochara* was studied in detail by Gack and Peschke (1994, 2005). The gonopore is located at the base of the flagellum. The flagellum is an intromittent tube that is inserted into the spermathecal duct of the female during copulation. It plays the role as the *guiding rod of an extension tube (or sperm)*. Note here that the extension tube is a very thin tube growing out from the spermatophore, to go through the spermathecal duct (Gack and Peschke 1994: Fig. 3).

In *Phanerota* (Ashe 1986), the copulatory tube is basically thin, and about as long as or distinctly longer than the whole length of the aedeagus, but the main tube seems to weakly differentiate into the stiff basal tube and the flexible, whiplike apical tube (e.g., Ashe 1986, Figs. 1, 8A and 9A). It belongs to form 3 or 4 (Fig. 13.4). At the dorsal side of the demarcation part of the copulatory tube between the basal and the apical tube, there exists a small pointed hook. On the other hand, the spermatheca of the female is moderately long and loosely coiled; and there exists a small triangular chamber at one side of the opening of the spermathecal duct (Ashe 1986, Fig. 7). Since the hook of the male copulatory tube nearly fits the triangular chamber of the spermatheca in size, the triangular chamber seems to function as the container for receiving the hook during copulation. It is thus hypothesized that the flexible, whiplike apical tube only is inserted into the spermathecal duct; and the pointed hook of the copulatory tube is pocketed into the triangular chamber of the spermatheca so that the copulatory tube tightly fixes in position during copulation.

13.6.1.5 Form 5 of Copulatory Tube

Given the thickness of the basal tube of the main tube in the form 5 (Fig. 13.4), the basal tube is considered to function as the chamber for storing a spermatophore (or sperm), as in the form 6 (e.g., Fig. 13.6g). It means that a spermatophore goes through the basal tube until near its tip before it is transmitted to the female genital chamber. Thus, the gonopore is supposed to be located at or near the tip of the thick basal tube in *Stenus* (Fig. 13.4). In *Stenus ebisu* (Fig. 13.5g, i) and its allied species (e.g., *S. olliformis*; Fig. 13.5f), the apical tube seems to play a role as an intromittent organ into the spermathecal duct; and it may also serve as a rod guiding an extension tube (growing out from a spermatophore), because of the following two reasons: first, the length and width of the apical tube (Fig. 13.5g) just fit the length and width of the female spermathecal duct from the opening to the base of the basal valve (Fig. 13.5h); and second, the cross section of the apical tube is -U-shaped (Fig. 13.5g) as in the flagellum of *Aleochara*, which functions as the guiding rod of an extension tube.

13.6.1.6 Form 6 of Copulatory Tube

It was observed during my morphological studies that a spermatophore is deposited near the apex of the main tube in a male of *Stenus gyrosus* Naomi 2006b (Fig. 13.6f, g). This certainly implies that the gonopore of this *Stenus* species is located at or near the tip of the main tube (Fig. 13.4). The copulatory tube of *S. gyrosus* is so strongly sclerotized and rigid that a spermatophore may safely pass through the main tube to the gonopore, without its deformation.

Given the thickness of the main tube, it is apparent that the form 6 (Fig. 13.4) is not an intromittent organ into the spermathecal duct. In a female of *S. ichihashii* (whose male has a form 6 of a copulatory tube), a large spermatophore was observed that is probably pasted by a male at the opening of the spermathecal duct during copulation (Fig. 13.7). This observation suggests that the copulatory tube is supposed to function as the *spermatophore* (*or sperm*) *depositor*; here the spermatophore (or sperm) depositor means a rod or stick that directly deposits a spermatophore (or sperm) in the vagina or in the female basal pouch or infundibulum (i.e., a bowl-like pouch located at the opening of the spermathecal duct; Fig. 13.6b). Thus, in *Stenus* the sperm is transferred from the vagina to the spermatheca after the copulation, as in *Aleochara* (Gack and Peschke 1994). The apicomedian protuberance (Fig. 13.6a, d, e, g) probably has a function of fixing the main tube in position during copulation, by putting it into the opening of the spermathecal duct, because the size of the apicomedian protuberance just matches the size of the opening of the spermathecal duct. One might compare, for example, the size of the apicomedian protuberance of the copulatory tube in *S. ichihashii*, (Fig. 13.6a) with the size of the opening of spermathecal duct of the same species (Fig. 13.6b).

13.6.1.7 Form 7 of Copulatory Tube

In *Dianous* (Fig. 13.6i; Puthz 2000a) and *Stenus* (Fig. 13.6h; Naomi 2010), there exists a large opening at the apicomedian part of the copulatory tube (Fig. 13.4), which is considered the gonopore. A spermatophore (or sperm) is stored in the large basal chamber, whereas the main tube is supposed to play the role of fixing a copulatory tube in position during copulation, given the occurrence of various modifications (e.g., accessory lobes and projections) at the lateral and/or apical parts of the main tube. When considering the aforementioned function, together with the thickness of the main tube, the form 7 is considered to function as a spermatophore (or sperm) depositor.

In some *Dianous* species with an atrophied main tube (Fig. 13.6i), the basal chamber seems to become very large as if it were the main tube; and thus a possible interpretation of it is that the atrophy of the main tube is compensated by the enlargement of the basal chamber. If my interpretation is correct, then it seems in such cases that the basal chamber of form 7 functionally plays a similar role in the basal tube of form 6 (e.g., Fig. 13.6g), while the reduced main tube of form 7 plays a similar role in the apicomedian protuberance (as a reduced apical tube) of form 6 (e.g., Fig. 13.6g) in a sense that it has a role of fixing the copulatory tube in position during copulation.

13.6.2 Summary on the Functions of Endophallic Copulatory Tubes

What we understood and hypothesized about the functions of copulatory tubes in Staphylinidae are here summarized.

The functional gonopore is located at the base of the copulatory tube in the form 1, 2, and 4, at or near the base of the copulatory tube in the form 3, at or near the apex of the basal tube in the form 5, near the apex of the main tube in the form 6, and at the apicomedian part of the main tube in the form 7.

We can certainly demonstrate that the forms 1–7 of the copulatory tube all have the function of transferring a spermatophore (or sperm) to the vagina and then to the spermatheca of a female.

However, strictly, the presented analyses suggest the following functions of copulatory tubes: (1) the form 1r (e.g., some *Thinobius*) and 6 and 7 (e.g., some *Stenus*, *Dianous*), which each comprises of a thick or very thick copulatory tube, are not intromittent organs into the spermathecal duct. Each serves simply as the spermatophore (or sperm) depositor, that is, a stick or a swell that directly deposits the spermatophore (or sperm) into the vagina or into the basal pouch located at the opening of the spermathecal duct; (2) the forms 1sa, 1sb, 2rb, 2s, and 3–5 each play a role as an intromittent organ into the spermathecal duct, because the apical portion or the apical tube of the copulatory tube is made up of a thin tube. The spermatophore (or sperm) is deposited in the vagina by the copulatory tubes of these forms. At least the forms 3–5 each are, given their structures (Fig. 13.4), supposed to serve also as an extension tube (or sperm) guiding rod, that is, a rod that guides the spermatophore extension tube (or sperm) into the spermathecal duct, as shown in *Aleochara* by Gack and Peschke (1994). Thus, the functions of the copulatory tubes are double in such cases (e.g., some *Aleochara*, *Stenus*): a "spermatophore (or sperm) depositor" and an "extension tube (or sperm) guiding rod"; (3) the function of the form 2ra is unclear.

Acknowledgments I would like to express my sincere gratitude to Dr. Alessandro Minelli (Padova University) and to Dr. Margaret Thayer (Field Museum) for their constructive and also critical comments on my earlier versions of the draft of this paper and to Dr. Yoko Matsumura (Hokkaido University) for her useful discussion with me about the morphology of the flagellum in Coleoptera. I sincerely thank Dr. Volker Puthz (Schlitz) for his kindness in sending me some valuable *Stenus* specimens for this study and also for informing me of some interesting forms of *Stenus* flagella, Dr. Alexey Shavrin (Daugavpils University) for letting me know valuable information on the copulatory tubes in Omaliinae, and Dr. Volker Assing (Hannover) for informing me of the matter with the paederine flagellum. My hearty thanks are due to Dr. Munetoshi Maruyama (Kyushu University Museum) for providing important information on the morphology of the coleopterous flagellum and to Dr. Hiroyuki Yoshitomi (Ehime University) for his advices for this study in various ways. Finally I sincerely thank the editors of this book for improving the manuscript of my paper in various ways.

References

Abarbanell NR, Ashe JS (1989) Revision of the species of *Pinophilus* Gravenhorst (Coleoptera: Staphylinidae) of America north of Mexico. Field Zool 54:1–32

Ahn KJ (1996) A review of *Diaulos* Casey (Coleoptera: Staphylinidae: Aleocharinae), with description of a new species and known larvae. Col Bull 50:270–290

Ahn KJ (1997) A review of *Liparocephalus* Mäklin (Coleoptera: Staphylinidae: Aleocharinae), with descriptions of larvae. Pan-Pacif Ent 73:79–92

Ahn KJ (2001) Phylogenetic relationships of the intertidal genus *Halorhadinus* Sawada and key to the genera of the Liparocephalini (Coleoptera: Staphylinidae: Aleocharinae). Insect Syst Evol 32:123–132

Ahn KJ, Ashe JS (1996) A revision of *Rothium* Moore and Legner (Coleoptera: Staphylinidae: Aleocharinae) with a discussion of its phylogenetic relationships. J Kansas Ent Soc 69:234–256

Arai S, Nomura S (2003) Discovery of the tribe Odontalgini (Coleoptera: Staphylinidae; Pselaphinae) in Japan. Ent Sci 6:193–197

Ashe JS (1984) Generic revision of the subtribe Gyrophaenina (Coleoptera: Staphylinidae: Aleocharinae) with review of the described subgenera and major features of evolution. Quaest Ent 20:129–349

Ashe JS (1986) *Phanerota cubensis* and *Phanerota brunnessa* n. sp., with a key to the species of *Phanerota* occurring in Florida (Coleoptera: Staphylinidae). Florida Ent 69:236–245

Ashe JS (1992) Phylogeny and revision of genera of the subtribe Bolitocharina (Coleoptera: Staphylinidae: Aleocharinae). Univ Kansas Sci Bull 54:335–406

Ashe JS (2003) First record and four new species of *Adelarthra* Cameron 1920 from Australia, and a related new genus and species *Notiomerinx zealandica*, from New Zealand (Coleoptera: Staphylinidae: Aleocharinae). In: Cuccodoro G, Leschen RA (eds) Systematics of Coleoptera: Papers celebrating the retirement of Ivan Löbl. Memoirs on Entomology International 17:617–636

Ashe JS, Newton AF Jr (1993) Larvae of *Trichophya* and phylogeny of the tachyporine group of subfamilies (Coleoptera, Staphylinidae) with a review, new species and characterization of the Tachyporinae. Syst Ent 18:267–286

Assing V (1999) A revision of *Othius* Stephens (Coleoptera, Staphylinidae). VIII. Further records, new species, and a new synonym. Linzer biol Beitr 31:661–691

Assing V (2001) The first record of *Dinusa* Saulcy 1864 from Turkey (Coleoptera: Staphylinidae, Aleocharinae). Linzer biol Beitr 33:187–190

Assing V (2002) On some micropterous species of Athetini from Nepal and China (Coleoptera: Staphylinidae, Aleocharinae). Linzer biol Beitr 34:953–969

Assing V (2003) A revision of *Zoosetha* Mulsant & Rey and *Poromniusa* Ganglbauer. II. A new species from Spain and additional records (Coleoptera: Staphylinidae: Aleocharinae). Zootaxa 310:1–8

Assing V (2006) A revision of the Palaearctic species of *Orphnebius* Motschulsky (Coleoptera: Staphylinidae: Paederinae). Ent Prob 36:1–26

Assing V (2012) On the taxonomy and zoogeography of some *Oxypoda* species of the West Palaearctic region (Coleoptera: Staphylinidae: Aleocharinae). Linzer biol Beitr 44:365–399

Assing V (2013) On the Palaearctic and Oriental species of *Scymbalium* and *Micrillus* (Coleoptera: Staphylinidae: Paederinae). Linzer biol Beitr 45:1479–1520

Assing V (2014) A revision of the species of *Pinobius* MacLeay, 1871 of the Oriental, Palaearctic, and Australian Regions (Coleoptera: Staphylinidae: Paederinae). Kol Rund 84:115–191

Assing V, Wunderle P (1995) A revision of the species of the subfamily Habrocerinae (Coleoptera: Staphylinidae) of the world. Rev Suisse Zool 102:307–359

Blackwelder R (1936) Morphology of the coleopterous family Staphylinidae. Smith misc coll 94:1–102

Bordoni A (2002) Xantholinini della Regione Orientale (Coleoptera: Staphylinidae). Classificazione, filogenesi e revisione tassonomica. Museo Regionale di Scienze Naturali Monografie Turin 33:1–998

Bordoni A (2011) Notes on Palaearctic Xantholinini. VI. New species and new records from Caucasus (Coleoptera: Staphylinidae). Fragm ent 43:41–56

Brunke AJ, Chatzimanolis S, Schillhammer H, Solodovnikov A (2016) Early evolution of the hyperdiverse rove beetle tribe Staphylinini (Coleoptera: Staphylinidae: Staphylininae) and a revision of its higher classification. Cladistics 32:427–451

Clarke DJ, Grebennikov VV (2009) Monophyly of Euaesthetinae (Coleoptera: Staphylinidae): phylogenetic evidence from adults and larvae, review of austral genera, and new larval description. Syst Ent 34:346–397

Coiffait H (1972) Coléoptères Staphylinidae de la région Paléarctique occidentale. I. Suppl Nouv Rev Ent 2:1–651

Coiffait H (1974) Coléoptères Staphylinidae de la région Paléarctique occidentale. III. Suppl Nouv Rev Ent 4:1–593

Crowson RA (1981) The biology of the Coleoptera. Academic Press, London

Frisch J (1997) A revision of some West Palaearctic species of *Scopaeus* Erichson (Coleoptera, Staphylinidae, Paederinae). Rev Suisse Zool 104:523–557

Frisch J (1998) A revision of some West Palaearctic species of *Scopaeus* Erichson (Coleoptera, Staphylinidae, Paederinae). Rev Suisse Zool 105:89–124

Frisch J (1999) A revision of the *Scopaeus debilis* species group, with description of a new species from Madagascar (Coleoptera, Staphylinidae, Paederinae). Rev Suisse Zool 106:361–383

Frisch J (2003) A revision of the *Scopaeus laevigatus* species group, with descriptions of ten new species from the East Palaearctic, the Oriental and the Australian regions (Coleoptera, Staphylinidae, Paederinae). In: Cuccodoro G, Leschen RA (eds) Systematics of Coleoptera: Papers celebrating the retirement of Ivan Löbl. Memoirs on Entomology International 17:649–726

Gack C, Peschke K (1994) Spermathecal morphology, sperm transfer and a novel mechanism of sperm displacement in the rove beetle, *Aleochara curtula* (Coleoptera, Staphylinidae). Zoomorphology 114:227–237

Gack C, Peschke K (2005) 'Shouldering' exaggerated genitalia: a unique behavioural adaptation for the retraction of the elongate intromittent organ by the male rove beetle (*Aleochara tristis* Gravenhorst). Biol J Linn Soc 84:307–312

Gusarov V (2003) Revision of some types of North American aleocharines (Coleoptera: Staphylinidae: Aleocharinae), with synonymic notes. Zootaxa 353:1–134

Hammond PM (1973) Notes on British Staphylinidae 3. The British species of *Sepedophilus* Gistel (*Conosomus* auctt.) Ent Mon Mag 108:130–165

Hemming BS (2003) Insect development and evolution. Cornell University Press, New York

Herman LH (1972) A revision of the rove-beetle genus *Charhyphus* (Coleoptera, Staphylinidae, Phloeocharinae). Am Mus Nov 2496:1–16

Herman LH (1975) Revision and phylogeny of the monogenetic subfamily Pseudopsinae for the world (Staphylinidae, Coleoptera). Bull Am Nat Hist 155:245–317

Herman LH (1981) Revision of the subtribe Dolicaonina of the New World, with discussions of phylogeny and the old world genera (Staphylinidae, Paederinae). Bull Am Mus Nat Hist 167:327–520

Hlaváč P, Nomura S (2001) A taxonomic revision of Tyrini of the Oriental region 1. *Paralasinus* (Coleoptera, Staphylinidae, Pselaphinae), a new genus of Tyrina from Indochina. Elytra 29:163–174

Hoebeke ER, Ashe JS (1994) New species of *Autalia* Leach 1819 from the Neotropics (Coleoptera Staphylinidae Aleocharinae), with new distributional data for *A. phricotrichosa* Hoebeke 1988 and key to the Neotropical species of *Autalia*. Tropical Zool 7:191–208

Hoshina H, Sugaya H (2003) New records of the genera *Scaphobaeocera* and *Scaphoxium* (Coleoptera: Staphylinidae) from the Ryukyus, Japan, with descriptions of two new species. Ent Rev Jpn 58:35–41

Hwang WS, Ahn KJ (2000) Taxonomy of the Korean Oxyporinae (Insecta, Coleoptera, Staphylinidae). Korean J Syst Zool 16:191–202

Irmler U (1981) Descriptions of new neotropical *Holotrochus* and a key to the species of the genus (Coleoptera: Staphylinidae). Col Bull 35:379–397

Irmler U (1985) Neue Arten der Gattungen *Aueucamptus* und *Thoracophorus* (Col., Staphylinidae) aus der Neotropis. Ent Blät 81:41–58

Irmler U (2005) New neotropical species of the genus *Holotrochus* (Coleoptera: Staphylinidae: Osoriinae). Sci Pap Nat Hist Mus Univ Kan 36:1–18

Jałoszyński P (2010) Cephenniini of the Philippines. Part 3. New species of *Cephennomicrus* Reitter and *Hlavaciellus* Jałoszyński from Palawan (Coleoptera: Staphylinidae: Scydmaeninae). Genus 21:13–20

Jałoszyński P, Nomura S (2009) The Cephenniini (Coleoptera, Scydmaenidae) of Vietnam. Bull Natl Mus Sci Ser A 35:167–225

Jeannel R (1959) Révision des Psélaphides de l'Afrique intertropicale. Ann Mus r Congo Belge Tervuren Ser 8 Sci Zool 75:1–742

Kanao T, Maruyama M, Hashim R (2011) A new genus of Compactopediina (Coleoptera: Staphylinidae) associated with *Longipeditermes* (Isoptera: Termitidae) in Peninsular Malaysia with a key to and phylogenetic analysis of all genera of the subtribe. Insect Syst Evol 42:349–364

Kim HJ, Ahn KJ (2000) A taxonomic review of the genus *Tachinus* Gravenhorst in Korea (Insecta: Coleoptera: Staphylinidae). Korean J Env Biol 18:125–131

Kishimoto T (2000) A new *Trigonurus* (Coleoptera: Staphylinidae, Trigonurinae) discovered in Sichuan, China. Elytra 28:305–309

Klimaszewski J (1984) A revision of the genus *Aleochara* Gravenhorst of America north of Mexico (Coleoptera: Staphylinidae, Aleocharinae). Mem Ent Soc Can 129:1–211

Kocian M (1996) A revision of Western Palearctic species of the genus *Ischnosoma* Stephens (Coleoptera: Staphylinidae, Tachyporinae). Acta Univ Carol Biol 40:241–299

Lawrence JF, Britton EB (1994) Australian beetles. Melbourne University Press, Carlton

Leschen RAB, Löbl I (2005) Phylogeny and classification of Scaphisomatini (Staphylinidae: Scaphidiinae) with notes on mycophagy, termitophyly, and functional morphology. Col Soc Monogr 3:1–63

Löbl I (2002) New species of *Scaphisoma* Leach (Coleoptera: Staphylinidae: Scaphidiinae) from Mt. Wilhelm, Papua New Guinea. Acta Zool Hung 48:181–189

Löbl I (2012) On Taiwanese species of *Baeocera* Erichson (Coleoptera: Staphylinidae: Scaphidiinae). Zool Stud 51:118–130

Löbl I (2015) On the Scaphidiinae (Coleoptera: Staphylinidae) of the Lesser Sunda Islands. Rev Suisse Zool 122:75–112

Löbl I, Burckhardt D (1988) *Cerapeplus* gen. n. and the classification of micropeplids (Coleoptera: Micropeplidae). Syst Ent 13:57–66

Löbl I, Calame FG (1996) Taxonomy and phylogeny of the Dasycerinae (Coleoptera: Staphylinidae). J Nat Hist 30:247–291

Löbl I, Mattila J (2010) *Euplectus lapponicus* (Coleoptera: Staphylinidae: Pselaphinae), a new species from boreal Finland. Ent Fenn 21:181–186

Makranczy G, Schülke M (2001) Typenstudien an den mitteleuropäischen Vertreten der Artengruppe des *Thinobius linearis* Kraatz, 1857 (Coleoptera, Staphylinidae, Oxytelinae). Ent Blät 97:185–193

Maruyama M (2000) A revision of the myrmecophilous genus *Aspidobactrus* (Coleoptera: Staphylinidae: Aleocharinae). Sociobiology 35:149–173

Maruyama M (2004a) Redescription of the genus *Creochara* (Coleoptera: Staphylinidae: Aleocharinae: Aleocharini) and its systematic position. Can Ent 136:621–637

Maruyama M (2004b) Taxonomy of the myrmecophilous genus *Myrmecopella* Kistner with descriptions of seven new species (Coleoptera: Staphylinidae: Aleocharinae). Kol Rund 74:201–219

Maruyama M (2006) Revision of the Palearctic species of the myrmecophilous genus *Pella* (Coleoptera: Staphylinidae: Aleocharinae). Nat Sci Mus Monogr Tokyo 32:1–207

Maruyama M (2008) *Giraffaenictus eguchii* (Coleoptera, Staphylinidae, Aleocharinae), a new genus and species of fully myrmecophile from a colony of *Aenictus binghami* (Hymenoptera, Formicidae, Aenictinae) in Vietnam. Esakia 48:51–56

Maruyama M, Hlavác P (2003) A new genus and species of myrmecophilous Aleocharini from Morocco (Coleoptera, Staphylinidae, Aleocharinae), associated with *Aphaenogaster* (Hymenoptera: Formicidae: Myrmicinae). Ann Soc ent Fr (new ser) 39:225–228

Maruyama M, Klimaszewski J (2004) A new species of the myrmecophilous genus *Goniusa* (Coleoptera, Staphylinidae, Aleocharinae) from Canada. Elytra 32:315–320

Maruyama M, Matsumoto T, Itioka T (2011) Rove beetles (Coleoptera: Staphylinidae) associated with Aenictus laeviceps (Hymenoptera: Formicidae) in Sarawak: strict host specificity, and first myrmecoid Aleocharini. Zootaxa 3102:1–26

Maruyama M, Sugaya H (2002) A new species of *Tetrasticta* (Coleoptera, Staphylinidae, Aleocharinae) from Japan and Taiwan. Jpn J Syst Ent 8:17–21

Matsumura Y, Yoshizawa K (2012) Homology of the internal sac components in the leaf beetle subfamily Criocerinae and evolutionary novelties related to the extremely elongated flagellum. J Morph 273:507–518

Mckenna DD, Farrell BD, Caterino MS, Farnum CW, Hawks DC, Maddison DR, Seago AE, Short AEZ, Newton AF, Thayer MK (2015) Phylogeny and evolution of Staphyliniformia and Scarabaeiformia: forest litter as a stepping stone for diversification of nonphytophagous beetles. Syst Ent 40:35–60

Naomi S (1986) Taxonomic study on the subfamily Osoriinae (Coleoptera, Oxytelidae) from Japan, I. Elytra 14:33–42

Naomi S (1990) Comparative morphology of the Staphylinidae and the allied groups (Coleoptera, Staphylinoidea) XI. Abdominal glands, male genitalia and female spermatheca. Jpn J Ent 58:16–23

Naomi S (1996) Revision of the genus *Lispinus* Erichson and *Neolosus* Blackwelder (Coleoptera: Staphylinidae) from Japan. Jpn J Ent 64:762–771

Naomi S (1997a) A revision of the genus *Nacaeus* Blackwelder (Coleoptera: Staphylinidae) from Japan. Jpn J Ent 65:127–142

Naomi S (1997b) Taxonomic study on *Stenus wasabi* Hromádka and its allied species (Coleoptera; Staphylinidae; Steninae), with discussion on the internal structure of the aedeagus. Jpn J Ent 65:600–611

Naomi S (2006a) Taxonomic revision of the genus *Stenus* Latreille, 1797 (Coleoptera, Staphylinidae, Steninae) of Japan: species group of *S. indubius* Sharp. Jpn J Syst Ent 12:39–120

Naomi S (2006b) Taxonomic revision of the genus *Stenus* Latreille, 1797 (Coleoptera, Staphylinidae, Steninae) of Japan: species group of S. (*Hypostenus*) *rufescens* Sharp. Nat Hist Res Chiba Spec Issue 9:1–81

Naomi S (2010) Descriptions of two new species of the genus *Stenus* Latreille (Coleoptera: Staphylinidae: Steninae) from Chubu District, Central Japan. Nat Hist Res Chiba 11:35–40

Naomi S, Irmler U (2012) First record of the genus *Allotrochus* Fagel, 1955 (Coleoptera: Staphylinidae: Osoriinae) from the Oriental region, with description of the new species A. takahashii from Ishigaki Is., Nansei Islands, Japan. Biogeography 14:105–110

Naomi S, Maruyama M (1997) Revision of the genus *Sepedophilus* Gistel (Coleoptera, Staphylinidae, Tachyporinae) from Japan: species group of *S. glabratus* and *S. exiguus*. Ent Rev Jpn 52:61–71

Naomi S, Maruyama M (1998) A revision of the genus *Sepedophilus* Gistel (Coleoptera, Staphylinidae, Tachyporinae) from Japan: species group of *S. pedicularius*. Jpn J Syst Ent 4:51–75

Naomi SI, Nomura S, Puthz V (2017) The subfamily Steninae Macleay, 1825 (Coleoptera: Staphylinidae) of Japan. Part 1. *Dianous* and *Stenus* (*S. comma* group to *S. guttalis* group). Nat Sci Mus Monogr Tokyo 46:1–339

Nichols SW (1989) The Torre-Bueno glossary of entomology. New York Entomological Society, New York

Nomura S (1991) Systematic study on the genus *Batrisoplisus* and its allied genera from Japan (Coleoptera, Pselaphidae). Esakia 30:1–462

Nomura S (2001a) A taxonomic revision of the Japanese species of the genus *Pselaphogenius* (Coleoptera, Staphylinidae, Pselaphinae). Part 3, Species from central Honshu. Mem Natn Sci Mus Tokyo 37:279–291

Nomura S (2001b) Descriptions of two new species of the Clavigerine genus *Articerodes* (Coleoptera, Staphylinidae, Pselaphinae) from the Ogasawara Islans, Japan. Elytra 29:343–351

Nomura S (2010) A taxonomic revision of Asian genera and species of the tribe Dimerini (Coleoptera, Staphylinidae, Pselaphinae). Jpn J syst Ent 16:221–247

Nomura S, Sakcoowong W, Chanpaisaeng J (2011) Three new species of the genus *Megatyrus* (Coleoptera, Staphylinidae, Pselaphinae) from Thailand. Spec Publ Jpn Soc Scarab 1:121–129

Ogawa R, Löbl I (2016) A review of the genus *Xotidium* Löbl, 1992 (Coleoptera, Staphylinidae, Scaphidiinae), with descriptions of five new species. Dt Ent Zeit 63:155–169

Pace R (1999) Nuove specie del genere *Leptusa* Kraatz raccolte da Manfred Kahlen. Veröff Tiroler Land Ferd 79:207–214

Pace R (2009) Aleocharinae del cile raccolte dal Dr. P. M. Giachino (Coleoptera, Staphylinidae). Lavori Soc Ven Sc Nat 34:25–32

Pace R (2010) Thamiaraeini, Lomechusini, Oxypodini, Hoplandriini e Aleocharini di Taiwan (Coleoptera, Staphylinidae). Boll Mus Civ Stor Nat Verona 34:19–54

Peschke K (1978) Funktionsmorphologische Untersuchungen zur Kopulation von *Aleochara curtula* Goeze (Coleoptera, Staphylinidae). Zoomorphologie 89:157–184

Puthz V (1973) On some Neotropical Euaesthetinae (Coleoptera, Staphylinidae). Stud Neotr Fauna 8:51–73

Puthz V (1974) Bemerkungen über die Gattung *Edaphus* Motschulsky und über Kistnerische *Edaphus*-Arten nebst neuen und alten afrikanischen Euaesthetinen. Rev Zool Afr 88:749–770

Puthz V (1976) Zwei neue Gattungssynonyme und ein Nomen novum bei den Euaesthetinen (Coleoptera: Staphylinidae). Ent Scand 7:239–240

Puthz V (1977) Die Gattung *Octavius* Fauvel (Coleoptera: Staphylinidae) weltweit verbreitet! Opusc Zool Budap 14:105–126

Puthz V (1978) Bemerkungen über *Schatzmayrina* Koch (Coleoptera, Staphylinidae). Ent Blät 74:47–51

Puthz V (1979) Eine neue Euaesthetinengattung aus dem Himalaya (Coleoptera, Staphylinidae). Reichenbachia 17:9–14

Puthz V (1985a) Neue und alte neotropische *Edaphus*-Arten aus dem Genfer Museum (Coleoptera, Staphylinidae). Rev Suisse Zool 92:351–357

Puthz V (1985b) Neue *Octavius*-Arten aus Nordindien und aus dem Himalaya-Gebiet (Coleoptera: Staphylinidae). Revue suisse Zool 92:697–705

Puthz V (1986a) Eine neue Art der Gattung *Edaphosoma* Scheerpeltz. Reichenbachia 23:135–138

Puthz V (1986b) Fünf neue *Edaphus*-Arten aus Afrika (Staphylinidae, Coleoptera). Philippia 5:311–317

Puthz V (1986c) Neue Arten der Gattung *Octavius* Fauvel, 1872, aus Südafrika nebst einer Bestimmungstabelle der in der Äthiopis lebenden Gattungsvertreter (Coleoptera: Staphylinidae). Ann Trans Mus 34:185–201

Puthz V (1988a) Three new *Stenaesthetus* species from Ethiopia (Insecta, Coleoptera: Staphylinidae). Reichenbachia 26:9–13

Puthz V (1988b) Die Steninen von Borneo II (Coleoptera, Staphylinidae). Neue und alte Arten, vorwiegend aus den Ausbeuten des Genfer Naturhistorischen Museums. Rev Suisse Zool 95:631–679

Puthz V (1989a) Zwei neue Euaesthetinen von der Elfenbeinküste (Coleoptera, Staphylinidae). Ent Blät 85:75–77

Puthz V (1989b) The male of *Stictocranius mariae* (Hatch) (Coleoptera, Staphylinidae). Ent Blät 85:165–166

Puthz V (1989c) Eine neue *Octavius* -Art aus Sumatra (Coleoptera, Staphylinidae). Rev Suisse Zool 96:115–116

Puthz V (1992) Neue und alte afrikanische *Edaphus*-Arten (Insecta, Coleoptera, Staphylinidae: Euaesthetinae). Ent Abhand 55:13–33

Puthz V (1998) Neuweltliche *Euaesthetus*-Arten (Staphylinidae, Coleoptera). Phillipia 8:223–244

Puthz V (2000a) The genus *Dianous* Leach in China (Coleoptera, Staphylinidae). Rev Suisse Zool 107:419–559

Puthz V (2000b) Neue und alte neotropische Arten der Gattung *Stenus* Latreille (Staphylinidae, Coleoptera). Philippia 9:165–213

Puthz V (2000c) Aptere *Stenus*-Arten aus den mexikanischen Hochgebirgen (Coleoptera: Staphylinidae). Mitt internat-entomol Ver 25:103–127

Puthz V (2002) Revision der Gattung *Tamotus* Schaufuss, 1872 (Coleoptera, Staphylinidae). Z Arb Gem Öst Ent 54:115–125

Puthz V (2003a) Revision of the genus *Fenderia* Hatch, 1957 (Coleoptera, Staphylinidae). In: Cuccodoro G, Leschen RA (eds) Systematics of Coleoptera: Papers celebrating the retirement of Ivan Löbl. Memoirs on Entomology International 17:637–648

Puthz V (2003b) Neue und alte Arten der Gattung *Stenus* Latreille aus China (Insecta: Coleoptera: Staphylinidae: Steninae). Ent Abhand 60:139–159

Puthz V (2008a) *Stenus* Latreille und die segenreiche Himmelstochter (Coleoptera, Staphylinidae). Linzer biol Beitr 40:137–230

Puthz V (2008b) *Kiwiaesthetus*, a new genus of Euaesthetinae from New Zealand (Coleoptera: Staphylinidae). Z Arb Gem Öst Ent 60:59–69

Puthz V (2010) Die Gattung *Edaphosoma* Scheerpeltz, 1976 in China (Coleoptera, Staphylinidae). Ent Blät 106:289–306

Puthz V (2011a) Afrikanische *Stenaesthetus*-Arten (Coleoptera: Euaesthetinae). Linzer biol Beitr 43:793–812

Puthz V (2011b) Neue und alte Euaesthetinen (Coleoptera: Staphylinidae). Z Arb Gem Öst Ent 63:13–31

Puthz V (2012a) Über die neuweltlichen *Megalopinus*-Arten (Coleoptera: Staphylinidae). Linzer biol Beitr 44:613–834

Puthz V (2012b) Zwei neue Arten der Gattung *Nothoesthetus* Saíz aus Chile (Coleoptera: Staphylinidae). Mitt int ent Ver Frankfurt a M 37:159–162

Puthz V (2012c) Über die *Megalopinus*-Arten der Orientalis (Coleoptera: Staphylinidae). Linzer biol Beitr 44:1373–1430

Puthz V (2013) Übersicht über die orientalischen Arten der Gattung *Stenus* Latreille 1797 (Coleoptera, Staphylinidae). Linzer biol Beitr 45:1279–1470

Puthz V (2014) Nordamerikanische Arten der Gattung *Euaesthetus* Gravenhorst (Coleoptera, Staphylinidae). Linzer biol Beitr 46:845–876

Sharp D, Muir F (1912) The comparative anatomy of the male genital tube in Coleoptera. Trans Ent Soc Lond 1912:477–642

Shavrin A (2012) On the taxonomic placement of *Geodromicus pusillus* Coiffait, 1983 (Coleoptera: Staphylinidae: Omaliinae). Zootaxa 3552:66–68

Shimada T (2002) A new *Aploderus* (Coleoptera, Staphylinidae, Oxytelinae) discovered in central Japan. Spec Bull Jpn Soc Coleopt 5:233–239

Smetana A (1973) Die *Leptusa*-Arten der Tschechoslovakischen Republik einschließlich Karpatorußlands (Col., Staphylinidae). Stutt Beitr Naturk Ser A Biol 255:1–46

Snodgrass RE (1935) Principles of insect morphology. McGraw-Hill, New York

Steel WO (1964) Insects of Campbell Island. Coleoptera: Staphylinidae. Pac Ins Monogr 7:340–375

Steel WO (1966) A revision of the staphylinid subfamily Proteininae (Coleoptera) I. Trans R Ent Soc Lond 118:285–311

Thayer MK (1987) Biology and phylogenetic relationships of *Neophonus bruchi*, an anomalous south Andean staphylinid (Coleoptera). Syst Ent 12:389–404

Thayer MK (1997) *Proglypholoma aenigma* gen. et sp. nov., *Glypholoma* spp. nov. and new records, and a phylogenetic analysis of Glypholomatinae (Coleoptera: Staphylinidae). Ann Zool Warszawa 47:157–174

Thayer MK, Newton AF Jr (1978) Revision of the south temperate genus *Glypholoma* Jeannel, with four new species (Coleoptera: Staphylinidae: Omaliinae). Psyche 85:25–63

Williams SA (1976) The genus *Oligota* (Coleoptera, Staphylinidae) in New Zealand. New Zeal J Zool 3:247–255

Williams SA (1978) The genus *Oligota* Mannerheim (Col., Staphylinidae) in the Ethiopian region. Ent Mon Mag 114:177–190

Wunderle P, Assing V (2000) A revision of the European species of *Hygropetrophila* Bernhauer (Coleoptera, Staphylinidae, Aleocharinae). Ent Blät 96:31–40

Yamamoto S, Maruyama M (2012) Revision of the seashore-dwelling subgenera *Emplenota* Casey and *Triochara* Bernhauer (Coleoptera: Staphylinidae: genus Aleochara) from Japan. Zootaxa 3517:1–52

Zanetti A (2014) Taxonomic revision of North American *Eusphalerum* Kraatz, 1857 (Coleoptera, Staphylinidae, Omaliinae). Ins Mundi 379:1–80